Original research

The impact of natural resource use on bird and reptile communities within multiple-use protected areas: evidence from sub-arid southern Madagascar

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Abstract

Multiple-use protected areas, in which sustainable levels of extractive livelihood activities are permitted, play an increasingly important role in the global protected area estate, and are expected to rise in prevalence. However, we know little about their effectiveness at conserving biodiversity. We surveyed bird and reptile communities in three areas across a forest disturbance gradient resulting from charcoal production and shifting cultivation within a multiple-use protected area in Madagascar's sub-arid spiny forest. We scored individual species using a Conservation Value Index (CVI; a simple metric based on rarity, threat and distinctiveness), and estimated the total conservation value of each treatment by calculating the sum of frequency-weighted CVI scores across all present species. Bird and reptile community responses to forest disturbance were idiosyncratic. Bird richness was greatest in the moderate-disturbance treatment, but the low-disturbance treatment had the superior conservation value due to higher frequencies of locally-endemic species. Reptile richness was the same in low- and moderate-disturbance treatments, but the conservation value of the latter was greater. The high-disturbance areas had lowest richness and conservation value for both groups. For birds, increasing disturbance levels were accompanied by community turnover from high-value to low-value species, a pattern highlighted by CVI that is masked by assessing species richness alone. Although some endemic species appear to be resilient to degradation, multiple-use protected areas in Madagascar may lose biodiversity since most endemic species are forest-dependent. Stricter protected area models may be more appropriate in areas where much of the high-value biodiversity is sensitive to habitat degradation.

Keywords: Conservation value; Degradation; Dry forest; Faunal communities; Sustainable Use

1 Introduction

The impacts of human activity now threaten most of the Earth's species and ecosystems (Ehrlich and Pringle 2008) and have precipitated the planet's sixth mass extinction (Barnosky et al. 2011). Our primary strategy to stem this biodiversity loss is the creation and management of protected areas, which cover over 15 % of the world's land area and constitute the largest planned land use in history (Juffe-Bignoli et al. 2014). All protected areas are spaces "recognised, dedicated and managed... to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley 2008), but they vary greatly in management objective and approach. These differences form the basis for the World Conservation Union's (IUCN) protected area categorisation system (Dudley 2008; Dudley et al. 2010). For simplicity's sake the categories are often divided into 'strict' protected areas (generally categories I-IV), which seek to isolate nature from human processes that threaten it, and 'multiple-use' sites, which promote conservation through the sustainable extractive use of natural resources (category VI) or traditional land uses that sustain biodiversity (category V).

Recent decades have seen the number of multiple-use protected areas grow significantly in many parts of the world (Juffe-Bignoli et al. 2014). Although some strict sites have been downgraded (Mascia et al. 2014), this has been driven primarily by the predominance of multiple-use categories amongst new protected areas (Zimmerer et al. 2004). The trend can largely be attributed to: i) the lack of remaining 'wilderness' areas, with a low human footprint, suitable for the creation of strict categories (Leroux et al. 2010); and, ii) a paradigm shift in conservation, reflecting concern for the effects of exclusionary approaches on human wellbeing (Adams and Hutton 2007; Miller 2014), and the suggestion that sustainable use

may be a more effective long-term conservation strategy than strict protection (Rosser and Leader-Williams 2010). As a result, only 45 % of the world's protected areas are assigned to categories I-IV (Jenkins and Joppa 2009), and category VI sites expanded from 14 to 32 % of the world's protected area estate (by area) between 1990 and 2010 (Bertzky et al. 2012). This trend is expected to become even more pronounced in the future (McDonald and Boucher 2011).

Signatories to the Convention of Biological Diversity are expected to increase the coverage of terrestrial protected areas to 17 % of their national territory by 2020 and ensure that they are "effectively managed" (CBD 2010, Aichi Target 11), a target that will require the most rapid expansion of protected areas in history (Venter et al. 2014). Thus, if new protected areas are expected to largely comprise multiple-use categories, it is important to know whether they are likely to be successful at achieving their objective – the long-term conservation of nature – in the face of authorised human impacts (Dudley et al. 2014; Watson et al. 2016). This is particularly apposite given longstanding debates over the contribution of multiple-use protected areas to conservation goals (Locke and Dearden 2005; Gaston et al. 2008; Shafer 2015).

The effectiveness of protected areas depends on both their coverage (i.e. ensuring that maximum biodiversity is represented within them) and their success in buffering the biodiversity from the processes that threaten its viability (Gaston et al. 2008; Watson et al. 2014). However, research tends to concentrate on the former (e.g. Montesino Pouzols et al. 2014; Venter et al. 2014; Butchart et al. 2015; Polak et al. 2015; Visconti et al. 2015), with the result that we know little about the success of protected areas in maintaining their condition over time (Cabeza 2013; Geldmann et al. 2013; Beaudrot et al. 2016; Watson et al.

2016). This knowledge gap is particularly acute with regards to multiple-use categories. Global studies comparing across categories have found stricter protected areas to be more effective at slowing deforestation in some regions (Joppa and Pfaff 2011; Scharlemann et al. 2010), whereas multiple-use sites demonstrate greater success in other countries (Ferraro et al. 2013; Nelson and Chomitz 2011). However, the use of remote sensed data within such analyses only allows us to quantify vegetation cover, therefore providing little insight into the ecological integrity of remaining natural vegetation and faunal communities beneath the canopy (Peres et al. 2006; Beaudrot et al. 2016). Less conspicuous changes to forest structure and composition (i.e. forest degradation) can stem from activities such as non-industrial selective logging, fuelwood collection, livestock grazing and the harvesting of non-timber forest products (NTFPs). Typically, these are precisely the types of activity that may be sanctioned within category V and VI protected areas (Dudley 2008). Indeed, conservationists still have a very limited understanding of species and community responses to habitat change, and our knowledge is largely derived from a small number of sites (Barlow et al. 2007; T. Gardner et al. 2009, 2010). Furthermore, few researchers have investigated the impacts of subsistence activities on biodiversity (Borghesio 2008; Brown et al. 2013).

Madagascar is an example of a biodiversity-rich tropical developing country that is expanding its protected area system through the creation of new multiple-use sites. The island is a global conservation priority, boasting an unparalleled combination of species diversity and endemism (Brooks et al. 2006), with the majority of its endemic biota being forest dependent (Goodman and Benstead 2005). However, less than 16 % of the country retained forest cover by 2000 (Harper et al. 2007; McConnell and Kull 2014). Since 2003, Madagascar has been in the process of tripling the coverage of its protected area system, from 1.7 to over 6 million ha, in response to lobbying from international conservation

organisations and funders (Corson 2014). Known as the 'Durban Vision' after the location of the fifth World Parks Congress at which it was launched, this ambitious programme has necessitated modifications to the country's conception of protected areas and their governance. Previously, all protected areas were governed by the State, managed by the para-statal Madagascar National Parks, and comprised only strict categories (I, II and IV; Randrianandianina et al. 2003). Most of the new protected areas established as part of the Durban Vision are co-managed by non-governmental organisations (NGOs) and local communities, and are proposed or designated as categories V and VI (AGRECO 2012; Gardner 2011; Virah-Sawmy et al. 2014), with zoned areas where subsistence and low-level commercial natural resource use activities are permitted (e.g. Gardner et al. 2008; Virah-Sawmy et al. 2014; WWF 2010).

The goals of the expanded Madagascar Protected Area System (SAPM) are to conserve the country's unique biodiversity and its cultural heritage, as well as promoting the sustainable use of natural resources for poverty alleviation and development (Commission SAPM 2006). The simultaneous achievement of these goals is particularly complex because most forms of traditional land and resource use in Madagascar have negative impacts on biodiversity (Gardner 2009, 2011; Irwin et al. 2010). Planning the management of new multiple-use protected areas requires an understanding of species and community responses to habitat degradation arising from permitted resource use, yet our knowledge of the influence this has on biodiversity is patchy for the country as a whole, and particularly for the globally-important spiny forest ecoregion (Irwin et al. 2010). Moreover, existing studies in Madagascar tend to mirror patterns in global research (Burivalova et al. 2014) by summarising assemblage-level change via species richness (e.g. Randriamiharisoa et al. 2015; Scott et al. 2006). In other words, while studies may investigate the ecological or other

attributes of species remaining in degraded habitats, their results are usually reported in terms of species richness, but this measure has been criticised because it can mask community turnover from specialists to generalists (Barlow et al. 2007; Gardner et al. 2010). Here we investigate bird and reptile community responses to habitat change in a new protected area in the spiny forest ecoregion to ascertain the impacts of permitted and illegal livelihood activities (charcoal production and shifting cultivation respectively) on the conservation value of the vertebrate fauna. To overcome the issues associated with species richness as a metric, we use a novel Conservation Value Index (CVI) to examine the influence of habitat degradation on the two taxonomic assemblages.

2 Methods

2.1 Study site

Madagascar's spiny desert (or spiny forest), is a global priority ecoregion (Olson and Dinerstein 1998) and Endemic Bird Area (Stattersfield et al. 1998) with extremely high rates of local floral endemism (Phillipson 1996). Between 1990 and 2010 it suffered the fastest rates of deforestation of any ecoregion in the country (Harper et al. 2007; ONE et al. 2013) and, prior to 2003, it was the least represented ecoregion within the country's protected area network (Fenn 2003).

Ranobe PK32 is a new protected area that received temporary protected status within the Durban Vision framework in 2008, and is co-managed by local community associations, the regional Forest Service and the international NGO WWF (Virah-Sawmy et al. 2014). Lying north of the regional capital Toliara between the Fiherenana and Manombo rivers (Fig. 1), it is the richest landscape in the ecoregion in terms of its bird, reptile and lemur fauna (Gardner et al. 2009a,b; 2015a). However, the area is inhabited by approximately 90,000 people (WWF

2010), many of whom depend on natural resources from within and around the protected area for their subsistence and household income (Gardner and Davies 2014; Gardner et al. 2015b). Ranobe PK32 is thus proposed as a category VI protected area in which subsistence and low-level commercial livelihood activities (such as timber cutting, fuelwood collection and charcoal production, grazing and the harvesting of NTFPs) are permitted in sustainable use zones which cover 86.5 % of the protected area's 148,554 ha (Virah-Sawmy et al. 2014; WWF 2010).

Charcoal is primarily produced in the western part of the protected area, due to the presence of the Route Nationale 9 (RN9) road that facilitates transportation. The industry is driven by the close proximity of Toliara, a city of approximately 200,000 people in which 98 % of households use wood or charcoal for cooking; demand from the city tripled between 2000 and 2007, and is largely met by anarchic charcoal production along the RN9 (Gardner et al. 2015b; Partage 2008). Since the region lacks fuelwood plantations, charcoal is produced entirely from natural forests (Bertrand et al. 2010). Charcoal producers select only hardwood trees (Randriamalala et al. 2016), thus causing forest degradation rather than outright deforestation (Casse et al. 2004).

We conducted our study in the vicinity of Ranobe, a complex of three villages with a total population of approximately 2000 people (Gardner and Davies 2014), where the surrounding forests had been subjected to both charcoal production and shifting cultivation within recent years. We selected three areas within 3 km of the main village which, until recently, were part of a contiguous and relatively homogeneous forest block. Subsequently, the three areas have suffered varying levels of disturbance that are indicative of the habitat degradation gradient found across the whole landscape: i) a forest area showing minimal impacts of

human activity (low-disturbance, hereafter *Low*); ii) a forest area subject to intensive charcoal production (moderate-disturbance, *Mod*); and, iii) an area regenerating following shifting cultivation (high-disturbance, *High*). While *Low* and *Mod* retained a complex three-dimensional structure and can be termed forest, *High* was an open area dominated by shrubs, with only scattered trees (Fig. 1, Table 1). As there were no areas of forest near Ranobe that had not been subject to any human disturbance, it was not possible to include a control site representing intact habitat. Birds and reptiles were surveyed between January and March 2010 in the rainy season, when both groups are most active (Glaw and Vences 2007; Safford and Hawkins 2013).

[Fig. 1]

[Table 1]

2.2 Bird survey protocol

We established 48 census stations within each area and used the point count method (Bibby et al. 1998) to estimate bird relative abundance. Access to the forest interior was hindered by the impenetrable nature of the vegetation at *Low* and *Mod,* so census stations were placed on a stratified random grid along existing ox-cart tracks. We positioned all stations at a perpendicular distance of 75 m from a track (following Jones et al. 1995) to minimise the influence of edge effects, and at least 150 m apart to minimise the risk of double counting.

We surveyed each census station for 15 minutes (following a settling period of four minutes after arrival), during which we recorded all visual and auditory contacts within 50 m of the census station. To reduce time-of-day and weather-related effects, surveys were limited to

between 06.00 and 08.00 and were not conducted on rainy or windy days. The majority of bird contacts in spiny forest (> 85 % at *Low* and *Mod*) were auditory due to the dense vegetation, thus making it difficult to generate reliable distance estimates for bird contacts and, as such, we did not employ distance sampling methods. However, the non-visual nature of most contacts reduces the likelihood of a detectability bias arising from surveying in forests of varying degradation levels (Bibby and Buckland 1987). The auditory nature of most contacts also meant that we could not accurately count the number of individuals for social species, and thus we recorded the presence of groups not individuals. We did not include contacts with juvenile birds in our data analysis to reduce seasonality effects. Point count observations yielded both relative frequency (defined as the proportion of counts in which a given species was recorded) and relative abundance (mean number of contacts of a given species per count) data.

2.3 Reptile survey protocol

We calculated the relative abundance of reptiles based on capture in pitfall traps and area constrained refuge searches (transects), because observation and capture-based methods permit the sampling of different components of the reptile fauna (Raselimanana 2008). For pitfall trapping we followed a standard protocol widely used in Madagascar (D'Cruze et al. 2007; Raselimanana 2008). The traps consisted of plastic buckets (270 mm deep, 290 mm internal diameter at top, 220 mm internal diameter at base) placed 10 m apart and buried in the ground with the rim level with the surface. Drainage holes were drilled in the bottom of each bucket and the handles were removed. Buckets were connected by a drift fence 500 mm high, passing directly over the centre of each bucket, constructed from a sheet of plastic supported by wooden stakes. The lower 50 mm of the fence was buried in the soil and covered with leaf litter to prevent animals passing underneath. Within each treatment we

established three trap lines (each of 10 or 11 buckets), placed randomly, but at least 150 m apart. Traps were constructed in the morning and left open for 13 nights, equating to 403 trap nights in total per area, and were checked at 07.00 and 16.00 each day. All captured animals were marked on the hind leg or ventral surface with nail polish, and released at the site of capture. Recaptured individuals were excluded from the data analysis.

We also established 38 transects along which we conducted active refuge searches. Each transect consisted of a 50 m rope erected adjacent to forest tracks based on a stratified random grid. Each transect was at least 150 m apart, ran perpendicular to a track and started 10 m into the forest to reduce the influence of edge effects. We established each transect 24 hours prior to surveying to minimise disturbance effects. During surveys, two observers moved slowly along each transect and searched for reptiles within 2 m of the central line, scanning the trunks and branches of trees, searching within tree holes, under bark, in the leaf litter and under/within dead branches. All reptiles initially observed within 2 m of the central line were recorded. Transects were walked from 08.00-10.00 (n = 22/site) and 15.00-17.00 (n = 16/site); we did not survey during periods of rain or thick cloud cover to minimise variation in weather-related detectability, which reduced the number of appropriate afternoon survey periods. Juveniles were omitted from the dataset to minimise any bias that might be associated with the effects of the breeding season. Transects and pitfalls generated density and capture rate data, respectively: we pooled the data and used total contacts for further analyses (not including rarefaction).

2.4 Data analysis

In order to compare species richness between treatments and estimate the completeness of our sampling, we generated individual-based observed species richness rarefaction curves

and associated 95 % confidence intervals using EstimateS v.9.0 (Colwell 2013). For reptiles, we combined the two datasets by assigning species to one or other method on the basis of substrate use, following a protocol adapted from Bicknell et al. (2015), whenever a species was recorded by both methods. Thus all arboreal species were assigned to transects and all terrestrial and fossorial lizards were assigned to pitfall traps. Remaining terrestrial species (snakes and a tortoise) were assigned to the method by which they were most frequently recorded. We used chi-squared contingency tables to test for homogeneity of observed species relative frequency (birds) or total contacts (reptiles) across treatments.

Conservation Value Index

All species are not equal, and may differ in their value to conservationists on the basis of endemism, extinction risk (Mace et al. 2008), evolutionary distinctiveness (Tucker et al. 2012; Hidasi-Neto et al. 2015), public appeal (Smith et al. 2012) or other attributes (Humphries et al. 1995; Joseph et al. 2009). This variation forms the basis of a range of protocols designed to elucidate the conservation value of species and, in turn, support the prioritisation of conservation actions or funding allocations (e.g. Huang et al. 2016; Isaac et al. 2007; Joseph et al. 2009). However, these protocols tend to be methodologically complex and require the collection of large datasets, diminishing their applicability in situations where non-academic conservation practitioners lack the training to apply them or where the necessary data are unavailable (Gardner et al. 2015a). In this study, we therefore used the novel Conservation Value Index (CVI) (adapted from Gardner et al. 2015a) to quantify the conservation value of individual species because it uses only readily available data and does not require the use of specialist software. As such, it can be easily applied in day-to-day decision-making by conservation practitioners. We assigned CVI scores to individual species

300 of bird and reptile before combining them to assess the impacts of natural resource use, and
301 subsequent habitat degradation, on the conservation value of spiny forest habitats.
302
303 For the CVI we assigned scores to each individual species based on four attributes that reflect
304 rarity, distinctiveness and threat. We use different combinations of attributes for the two
305 taxonomic groups because the variation in conservation value within each group is driven by
306 different factors. We scored rarity using geographical scale of endemism (*G*) and
307 representation within SAPM (*R*), distinctiveness by taxonomic level of endemism (*E*), and
308 threat on the basis of hunting and collection pressure (*C*) and degradation tolerance (*T*). We
309 did not use *E* for reptiles because all species are endemic and there are no endemic families,
310 so variation in the attribute is limited. Similarly, we did not use *C* for birds because most
311 species in the Ranobe area are subject to comparable hunting pressure (Gardner and Davies
312 2014).
313
314 Introduced species were removed from the dataset and scores assigned to indigenous taxa on
315 a scale of 1-5 for each attribute (Table 2). For *G* we used different scoring systems for
316 reptiles and birds because species distributions of the two taxonomic groups are best
317 explained by different biogeographical models (Pearson and Raxworthy 2009). For birds we
318 used distribution maps from Safford and Hawkins (2013) and followed Stattersfield et al.
319 (1998) to classify microendemic species, whereas for reptiles we visually estimated range
320 criteria using maps in Glaw and Vences (2007) and adopted 10,000 km^2 as the threshold for
321 microendemic species (following Gardner et al. 2015a). *E* was assigned on the basis of
322 taxonomy in Safford and Hawkins (2013), *R* scores were assigned on the basis of occurrence
323 in 14 (birds) or 15 (reptiles) protected areas in the dry regions of Madagascar derived from
324 the literature (Online resource 1), and values for *C* were based on occurrence in CITES

(Convention on International Trade in Endangered Species) appendices and the literature on reptile declines in Madagascar. *T* was attributed following the methods outlined in Gardner et al. (2015a) for reptiles, and were based on the literature (Safford and Hawkins 2013; Wilmé 1996) for birds. Species for which no degradation tolerance data were available were scored as intolerant on the basis of the precautionary principle.

[Table 2]

The individual species CVI scores were calculated, producing a value in the range of 4-100, using the following formulae for reptiles and birds:

$$CVIreptile = (G + R)x(C + T)$$

$$CVIbirds = (G + E)x(R + T)$$

The conservation value of a site can be considered a function of: i) the value of the species occurring there; and, ii) their abundance, because an area with a large population of a valuable species is more important than one with a small population. To understand the relative conservation value of each habitat treatment, we therefore wanted a metric that combined the CVI of each species with their relative abundance. However, simply weighting the CVI score by the relative frequency would heavily bias common species at the expense of rarer ones which are recorded only infrequently. We thus gave each species weightings standardised to the treatment where it was most frequent (e.g., a species with relative frequency of 0.36, 0.18 and 0.12 across each of the three treatments would be given weightings of 1, 0.5 and 0.33 respectively). In each treatment the CVI was then multiplied by the weighting to produce a frequency-weighted CVI score for each species, before these were summed to produce a conservation value score for each treatment.

3 Results

3.1 Degradation impacts on birds

We recorded 2385 bird contacts, comprising 53 species, in point counts across all treatments. Rarefaction curves approach an asymptote in all treatments, indicating that bird communities were sufficiently sampled (Fig. S1). Although observed richness was highest in the moderate-degradation treatment (*Low* – 36 spp.; *Mod* – 43 spp.; *High* – 37 spp.), rarefaction curves show no significant differences in richness since the 95 % confidence intervals overlap (Online resource 2). Total richness is estimated at 42.0 (*Low*), 46.8 (*Mod*) and 39.7 (*High*) species in the three treatments. Twenty-four species (45.3 %) were recorded in all treatments, one species (1.9 %) was restricted to *Low*, five species (9.4 %) were restricted to *Mod*, and seven (13.2 %) species were restricted to *High*: 17 species (32.1 %) were recorded only in forest habitats (*Low* and *Mod*).

Observed patterns of species relative frequency differed significantly for 22 species (41.5 %) across the three treatments. Three of these species *(Cuculus rochii*, *Hypsipetes madagascariensis* and *Dicrurus forficatus*) were observed more frequently in the low-degradation treatment, one species (*Ploceus sakalava*) in the moderate-degradation treatment, and six species (*Turnix nigricollis*, *Oena capensis*, *Agapornis canus*, *Cisticola cherina*, *Acridotheres tristis* and *Foudia madagascariensis*) in the high-degradation treatment. A further 12 species were recorded less frequently in the high-degradation treatment than in forest habitat (*Low* or *Mod*) (Online resource 3).

Patterns of species endemism varied across the degradation gradient (Fig. 2). While the proportion of endemic species was approximately equal in all treatments, the high-

375 degradation treatment contained a lower proportion of regionally-endemic birds (defined as
376 restricted to Madagascar and the islands of the western Indian Ocean) and a higher proportion
377 of non-endemic species. The vast majority (97.9 %) of contacts with introduced species
378 (*Acridotheres tristis*) occurred in the high-degradation treatment.
379
380 [Fig. 2]
381
382 **3.2 Degradation impacts on reptiles**
383 We recorded 661 reptile contacts comprising 32 species, 27 of which were recorded at *Low*
384 and *Mod*, and 15 species at *High*. Twenty-two species were observed during transects, and 27
385 were captured in pitfall traps (Online resource 4). Twelve species (37.5 %) were recorded in
386 all treatments, 17 species (53.1 %) were only recorded in forest habitats, and one species
387 (*Lygodactylus tuberosus*) was recorded only in the high-disturbance site. Rarefaction curves
388 indicate that *Low* and *Mod* had significantly higher species richness than *High*, as there is no
389 overlap between confidence intervals (Online resource 5). Total richness is estimated at 30.5
390 (*Low*), 34.2 (*Mod*) and 19.1 (*High)* species in the three treatments.
391
392 Observed patterns of reptile abundance, based on total contacts, were significantly
393 heterogeneous for 11 species (34.4 %). Three species were recorded more frequently in the
394 low-degradation treatment (*Chalarodon madagascariensis*, *Lygodactylus verticillatus* and
395 *Oplurus cyclurus*), two species in the moderate-degradation treatment (*Madascincus* cf.
396 *igneocaudatus* and *Tracheloptychus petersi*), and three species in the high-degradation
397 treatment (*Lygodactylus tuberosus*, *Paroedura picta* and *Typhlops arenarius*). A further three
398 species (*Geckolepis* c.f. *polypelis*, *Phelsuma mutabilis* and *Trachylepis elegans*) were
399 recorded more frequently in the two forest areas than in the high-degradation treatment.

Forest disturbance affected distinct components of the reptile community differently, depending on their foraging substrate (Online resource 6). Terrestrial species decreased in frequency (capture rate and/or density) with increasing disturbance, while arboreal species demonstrated reduced frequency at *Mod* and reduced richness at *High* compared to the less degraded site. Fossorial and litter dwelling species reached peak frequency under conditions of moderate-intensity disturbance.

3.3 Conservation value of species and sites

The CVI allowed us to weight species on the basis of their conservation value. The six highest scoring bird species were locally-endemic forest specialists (Table 3), while the highest scoring reptile was the heavily harvested (and thus Critically Endangered) tortoise *Pyxis arachnoides* (Table 4). The relative conservation value of each treatment varied for the two taxonomic groups. Total bird conservation value was highest in *Low*, while total reptile conservation value was highest in *Mod*, although in both cases the differences between the two forest areas were small (Table 5). The high-degradation treatment had the lowest conservation value for both taxa.

[Table 3]

[Table 4]

[Table 5]

4 Discussion

We have generated some of the first data on the impacts of permitted livelihood activities within Madagascar's new generation of multiple-use protected areas. Our results show that charcoal production, an authorised activity within much of the Ranobe PK32 protected area, resulted in an overall reduction in the conservation value of habitats, although the responses of reptile and bird communities varied. However the impacts of charcoal production were less severe than the impacts of illegal shifting cultivation for both groups.

Although the impacts of habitat degradation on Madagascar's biodiversity have been well studied (reviewed in Gardner 2009; Irwin et al. 2010), the vast majority of research has been conducted in the country's humid and dry forests, ecosystems which greatly differ from the spiny forest in terms of biotic communities and abiotic conditions (Moat and Smith 2007; Goodman and Raherilalao 2013). Within the spiny forest, degradation has been found to reduce species richness in both birds (Randriamiharisoa et al. 2015) and reptiles (Theisinger and Ratianarivo 2015). However, in our study, richness was maintained for reptiles and increased for birds at moderate degradation levels. Indeed the conservation value of reptiles was greatest at the moderate-disturbance site, perhaps reflecting an increase in microhabitat heterogeneity or structural complexity (MacArthur and MacArthur 1961; Tews et al. 2004). Bird communities were more responsive than reptiles to habitat degradation, undergoing extensive community turnover. This was reflected in the greater prevalence of birds adapted to open areas, and a decrease in the frequency of certain high-value, locally-endemic species such as *Monias benschi*, *Coua cursor* and *Newtonia archboldi*, with increasing degradation intensity.

Wilmé (1996) suggests that "the tolerance of [Madagascar's] endemic forest avifauna to forest degradation is proportional to its degree of taxonomic endemism". However, we

recorded seven members of endemic genera (*Coua cursor*, *Monias benschi*, *Neomixis striatigula*, *Newtonia brunneicauda*, *N. archboldi*, *Vanga curvirostris* and *Xenopirostris xenopirostris*) previously thought to occur only in undisturbed or slightly disturbed habitats, within a largely deforested habitat in our high-disturbance treatment. These findings lend some support to the hypothesis that faunal species of Madagascar's dry and spiny forests may be more tolerant of degradation than those same or congeneric species in the country's humid east and north (Gardner 2009). This may arise due to the more 'gentle' habitat modifications occurring in dry forests compared to rainforests (Irwin et al. 2010): for example, the increased light penetration in forest gaps is thought to make little difference to the understory in the spiny forest, because the sparse, deciduous nature of the canopy already allows illumination at ground level (Seddon and Tobias 2007). However, while tropical dry forests are thought to be more resilient than humid forests in terms of regeneration capacity (Lebrija-Trejos et al. 2008), little is known about the relative disturbance sensitivity of their respective faunas. Such research should be considered a priority since it has important repercussions for the implementation of multiple-use protected areas in different bioclimatic contexts.

The finding that moderate levels of degradation provoked an increase in richness of birds, and maintained richness in reptiles, is consistent with Connell's (1978) 'intermediate disturbance hypothesis', and reflects a pattern widely reported from other tropical environments, at least for some guilds (Burivalova et al. 2014; Child et al. 2009; Gray et al. 2007; Martin and Blackburn 2010; Pons and Wendenberg 2005). However, all species are not equal, and the greater richness may often mask a turnover from range-restricted specialists to widespread generalists (Canaday 1997; Christian et al. 2009; Holbech 2005; Petit and Petit 2003; Scott et al. 2006). The latter are of less importance to conservationists precisely because they adapt well to anthropogenic disturbance and thus do not require conservation

actions, such as protected areas, to maintain them (Harris and Pimm 2004; T. Gardner et al. 2009). The use of species richness as a measure of conservation value has been widely criticised for this reason (Barlow et al. 2007; DeClercke et al. 2010; Fermon et al. 2005; Norris et al. 2010), but remains persistent (e.g., studies reviewed by Burivalova et al. 2014). Our use of the CVI provides further evidence of the inadequacies of richness in prioritising between sites or habitats, as the use of richness would indicate that forests degraded by charcoal production are more valuable for bird conservation in the spiny forest than less degraded habitats. Of course, the CVI does not represent a definitive quantification of conservation value, but is a useful heuristic tool to help conservationists prioritise action to where it is most needed (i.e. high-value species), and can be used without training, complex software or collecting new data.

Although the use of CVI provides novel insights into the impacts of habitat change on the conservation value of spiny forest bird and reptile assemblages, our results must be interpreted with caution. We carried out surveying during the rainy season when both groups are most active, and surveyed each site sequentially for logistical reasons. However, biases may have arisen due to changes in species detectability related to the advancing breeding season. In addition, the entry of new cohorts may have increased population size as surveying progressed. We minimised the latter problem by excluding all records of juveniles from the analysis, although it would have been preferable to repeat data collection over multiple years, or to survey each site simultaneously using multiple teams. Nonetheless, the latter approach has a number of drawbacks, including the extensive training needed to minimise the biases associated with potential differences in the bird detection abilities and/or identification skills of research assistants.

Although our observations appear to suggest that the majority of bird and reptile species in Ranobe are somewhat resilient to moderate or high levels of degradation, the presence of a species does not necessarily equate to its viability. It should not be assumed that local populations in disturbed areas will persist in the long-term because there are likely to be time lags associated with the impacts arising from perturbation, meaning that the degraded habitats at Ranobe may be carrying an 'extinction debt' (Kuussaari et al. 2009; Tilman et al. 1994). This is particularly true given that the habitat modifications that are the focus of this study are relatively recent (range: 3-15 years across the treatments). In addition, the persistence of some species within degraded habitats may be the result of source-sink dynamics, with populations maintained only by immigration from nearby areas of higher quality habitat (Hylander and Ehrlén 2013; Pulliam 1988; Tilman et al. 1994). The degraded habitats at Ranobe may therefore experience future local extinctions, even without further modification, and we may have over-estimated the value of these areas for bird and reptile diversity (Barlow et al. 2007; Sekercioglu et al. 2007). The scale of extinction debt can be influenced by habitat quantity, quality, or connectivity (Hylander and Ehrlén 2013). As such, when destructive activities such as charcoal production cannot be prevented within the 'sustainable use zones' of multiple-use protected areas, both the structural and functional connectivity between high-quality habitat patches should be maximised in order to maintain biodiversity and mitigate the negative impacts associated with resource exploitation.

The suggestion that Madagascar's new generation of multiple-use protected areas may suffer the continued erosion of biodiversity as a result of the impacts of authorised livelihood activities has important ramifications for the objectives and management of multiple-use sites worldwide. In a multi-taxon assessment across a continuum of protection levels in East Africa, Gardner et al. (2007) found that multiple-use protected areas provide significant and

complementary conservation services to strictly-protected sites, maintaining species richness but conserving significantly different faunal communities to those occurring in national parks. Thus a spectrum of protected area categories may be appropriate to conserve the full complement of biodiversity in continental regions, if these possess a range of faunal assemblages adapted to a continuum of habitat types from dense forests to wooded savannahs and grasslands (Borghesio 2008; Gardner et al. 2007; Pons et al. 2003).

Madagascar, however, differs from continents in that the vast majority of the endemic biota is forest-dependent (Goodman and Benstead 2005), while non-forest areas typically contain floristically- and faunistically-impoverished assemblages characterised by non-endemic species of low conservation value (Irwin et al. 2010; Koechlin et al. 1974; Lowry II et al. 1997). In this context, multiple-use sites essentially conserve the same communities as strict protected areas, but may do so less successfully than the latter. Thus, while multiple-use categories may be the only politically, ethically and logistically feasible option for many of Madagascar's new generation of protected areas, given the socioeconomic importance to rural communities of remaining forest resources (Gardner et al. 2013), it should not be assumed that they will be successful in maintaining the biodiversity they were established to conserve. Given that range-restricted habitat specialists are disproportionately likely to go extinct in modified habitats (Posa and Sodhi 2006; Scales and Marsden 2008), and are of greatest conservation interest worldwide, careful attention must be paid to the choice of protected area models in different contexts; in regions where the majority of priority species are disturbance-sensitive, strict protected areas may be a more appropriate model if they can be managed effectively.

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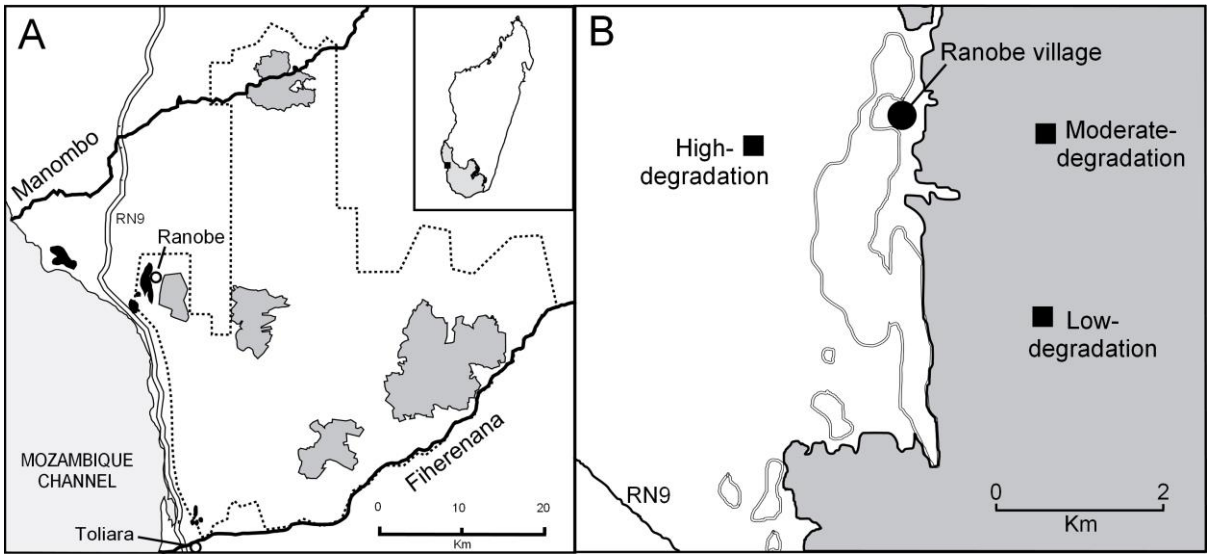
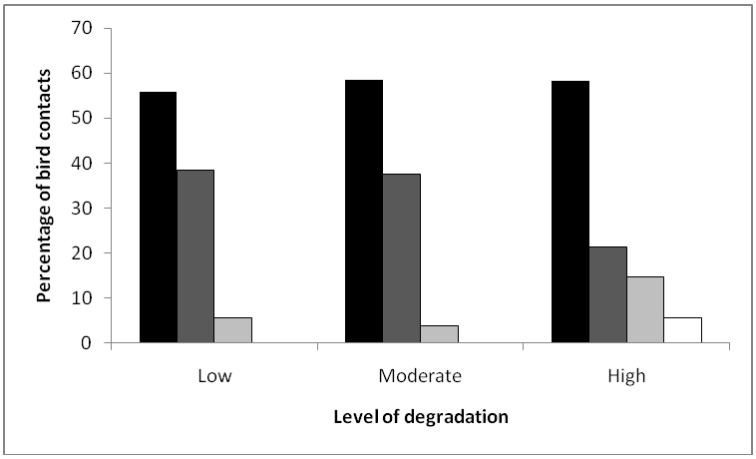
Figure Legends

Fig. 1 Map of: A) Ranobe PK32 protected area (dotted line) showing location of five strict conservation zones (grey shading), wetlands and rivers (black shading/lines) and Ranobe village; and, B) location of three vegetation treatments used to survey bird and reptile communities across a gradient of degradation (forest cover, grey shading; wetlands, double line). Inset shows location of Ranobe PK32 within Madagascar (black square) and limits of spiny forest ecoregion following Goodman and Raherilalao (2013) (grey shading)



990 **Fig. 2** Endemism status of birds at Ranobe expressed as a percentage of contacts from 48
991 point counts at three sites across a gradient of degradation. Black, Madagascar endemic; dark
992 grey, regional endemic; light grey, indigenous non-endemic; white, introduced. Regional
993 endemic species are defined as restricted to Madagascar and the western Indian Ocean islands
994 (Comoros, Mascarene and Seychelles archipelagos)



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996 **Table 1** Disturbance history and vegetation description of three habitat treatments used to
997 investigate the impacts of degradation on birds and reptiles at Ranobe, southwest
998 Madagascar.
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Treatment	Disturbance history	Habitat description
Low disturbance (*Low*)	Low level charcoal production since 2007	Relatively closed canopy dominated by *Didierea madagascariensis* and hardwood trees, with no understory shrub layer. Some charcoal production resulting in small openings, but canopy generally unbroken. Thick leaf litter layer.
Moderate disturbance (*Mod*)	Intensive charcoal production since 1995	Broken canopy dominated by *Didierea madagascariensis*, with hardwood trees largely absent. Small openings are frequent and possess a dense shrub layer of regenerating stumps. Characterised by piles of dead branches and bark left over from charcoal production. Thin leaf litter layer.
High disturbance (*High*)	Forest cleared for shifting cultivation in 2001, regenerating naturally since 2004/5	Dense shrub layer (height of 1-2m) of regenerating stumps dominated by *Cedrelopsis grevei* and *Fernandoa madagascariensis*, with no litter layer. Relict individual trees and small forest patches (< 1ha) occur within a mosaic pattern.

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Table 2 Scoring criteria for Conservation Value Index (CVI) attributes, used to quantify the conservation value of individual bird and reptile species at Ranobe, southwest Madagascar. EBA = Endemic Bird Area (Stattersfield *et al*. 1998), PA = protected area.

Taxonomic group	Score	Geographic scale of endemism (*G*)	Taxonomic level of endemism (*E*)	Representation in sample PAs (*R*)	Hunting/collection pressure (*C*)	Degradation tolerance (*T*)
Birds	**1**	Indigenous, non-endemic species	Indigenous, non-endemic species	Recorded in 12-14 PAs (n > 85%)	N/A	Tolerant of modified or artificial habitats
	2	Endemic to western Indian Ocean	Endemic species	Recorded in 8-11 PAs (55 > n < 85%)	N/A	N/A
	3	Widespread Madagascar endemic	Endemic genus	Recorded in 4-7 PAs (30 > n < 50%)	N/A	Tolerant of edge effects, medium-intensity degradation or secondary growth.
	4	Endemic to dry regions of Madagascar	Endemic subfamily	Recorded in 2-3 PAs (10 > n < 20%)	N/A	N/A
	5	EBA species	Endemic family	Recorded in only 1 PA (n < 10%)	N/A	Intolerant of low-intensity degradation
Reptiles	**1**	Indigenous, non-endemic species	N/A	Recorded in 12-15 PAs (n > 75%)	No known threat	Tolerant of modified or artificial habitats
	2	Widespread endemic, occurring in dry and humid regions	N/A	Recorded in 8-11 PAs (45 > n < 75%)	N/A	N/A
	3	Endemic to dry regions	N/A	Recorded in 4-7 PAs (20 > n < 45%)	Known threat (CITES Appendix I and II), but not known to cause local extirpations	Tolerant of edge effects, medium-intensity degradation or secondary growth.
	4	Endemic to one bioclimatic region[a]	N/A	Recorded in 2-3 PAs (10 > n < 20%)	N/A	N/A
	5	Local endemic, range size estimated as < 10,000 km^2	N/A	Recorded in only 1 PA (n < 10%)	Threat known to have caused local extirpations or severe population declines	Intolerant of low-intensity degradation

[a] Following Cornet 1974

Table 3 Bird species recorded at Ranobe showing attributes used in Conservation Value Index (CVI) and frequency-weighted CVI scores for three sites across a gradient of degradation: Low, Mod and High indicate low-, moderate- and high-degradation treatments. CVI attributes: *G* – geographic scale of endemism, *E* – taxonomic level of endemism, *R* – representation in sample protected areas, *T* – degradation tolerance. Asterisks indicate species endemic to the spiny forest Endemic Bird Area (Stattersfield *et al*. 1998).

Species	**CVI attribute scores**				**CVI**	**Frequency-weighted CVI**		
	G	**E**	**R**	**T**	**score**	**Low**	**Mod**	**High**
** Monias benschi*	5	5	4	5	**90**	90	22.5	22.5
** Xenopirostris xenopirostris*	5	5	3	5	**80**	0	11.4	80
** Coua cursor*	5	4	3	5	**72**	72	20.6	30.9
** Uratelornis chimaera*	5	5	4	3	**70**	0	0	0
** Thamnornis chloropetoides*	5	5	2	5	**70**	70	60.0	0
** Newtonia archboldi*	5	5	2	5	**70**	70	47.6	22.4
Coua ruficeps olivaceiceps	4	4	2	5	**56**	40.0	56	0
Calicalicus madagascariensis	3	5	2	5	**56**	56	56	0
Artamella viridis	3	5	2	5	**56**	32.0	56	0
Vanga curvirostris	3	5	1	5	**48**	48	29.2	4.2
Coua cristata	3	4	1	5	**42**	42	36.6	25.7
Falco zoniventris	3	2	3	5	**40**	0	40	0
Falculea palliata	4	5	1	3	**36**	36	36	0
Leptosomus discolor	2	5	2	3	**35**	0	0	0
** Nesillas lantzii*	5	2	2	3	**35**	35	0	11.7
Newtonia brunneicauda	3	5	1	3	**32**	32	30.7	14
Leptopterus chabert	3	5	1	3	**32**	19.2	16	32
Aviceda madagascariensis	3	2	3	3	**30**	0	30	0
Neomixis striatigula	3	3	2	3	**30**	21.5	30	10.8
Cuculus rochii	3	2	2	3	**25**	25	11.7	5
Polyboroides radiatus	3	2	1	3	**20**	20	10	0
Buteo brachypterus	3	2	1	3	**20**	0	20	0
Mirafra hova	3	2	3	1	**20**	0	0	20
Copsychus albospecularis	3	2	1	3	**20**	20	19.3	14.3
Treron australis	2	1	2	3	**15**	0	0	15
Nectarinia notata	2	1	2	3	**15**	0	15	3.75
Ploceus sakalava	4	1	2	1	**15**	0.7	15	5.0
Accipiter francesiae	2	1	1	3	**12**	0	12	0
Turnix nigricollis	2	1	1	3	**12**	2.1	0	12
Nesoenas picturata	2	1	1	3	**12**	9.7	12	2.9
Coracopsis vasa	2	1	1	3	**12**	12	12	0
Coracopsis nigra	2	1	1	3	**12**	5.0	12	0
Phedina borbonica	2	1	3	1	**12**	0	12	12
Hirundo rustica	1	1	5	1	**12**	0	0	0
Hypsipetes madagascariensis	2	1	1	3	**12**	12	2.6	6.8
Terpsiphone mutata	2	1	1	3	**12**	9.7	12	4.6
Neomixis tenella	3	3	1	1	**12**	12	11.7	9.3
Cisticola cherina	2	1	3	1	**12**	0	0	12
Nectarinia souimanga	2	1	1	3	**12**	11.5	12	8.8
Dicrurus forficatus	2	1	1	3	**12**	12	9	9.5
Falco peregrinus	1	1	4	1	**10**	0	0	10
Agapornis canus	3	2	1	1	**10**	3.3	3.3	10
Tachymarptis melba	1	1	4	1	**10**	0	10	0
Eurystomus glaucurus	1	1	2	3	**10**	0	10	0

Upupa marginata	3	2	1	1	**10**	10	6.4	8.6
Falco newtoni	2	1	2	1	**9**	4.1	3.3	9
Caprimulgus madagascariensis	2	1	2	1	**9**	9	0	0
Falco concolor	1	1	3	1	**8**	0	0	8
Foudia madagascariensis	3	1	1	1	**8**	0.2	0.8	8
Milvus migrans	1	1	2	1	**6**	0	0	0
Oena capensis	1	1	2	1	**6**	3.4	1.4	6
Centropus toulou	2	1	1	1	**6**	4.3	4.3	6
Apus barbatus	1	1	2	1	**6**	3	6	0
Merops superciliosus	1	1	2	1	**6**	3.7	3.3	6
Corvus albus	1	1	2	1	**6**	0	0	6
Numida meleagris	1	1	2	1	**6**	0	0	6
Total conservation value of treatment						**856.4**	**825.7**	**478.6**

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Table 4 Reptile species recorded at Ranobe showing attributes used in Conservation Value Index (CVI) score and relative frequency-weighted CVI scores for three sites across a gradient of degradation: Low, Mod and High indicate low-, moderate- and high-degradation treatments. CVI attributes: *G* – geographic scale of endemism, *R* – representation in sample protected areas, *C* – collection/hunting threat, *T* – degradation tolerance. Locally-endemic species are indicated by an asterisk.

	CVI attribute scores				CVI	Frequency-weighted CVI		
Species	**G**	**R**	**C**	**T**	**score**	**Low**	**Mod**	**High**
Pyxis arachnoides	4	3	5	5	**70**	70	0	0
** Voeltzkowia petiti*	5	4	1	5	**54**	14.7	54	0
** Tracheloptychus petersi*	5	4	1	5	**54**	22.1	54	2.5
Geckolepis polylepis	4	4	1	5	**48**	48	32.8	0
Paroedura androyensis	4	3	1	5	**42**	14	42	0
** Pygomeles braconnieri*	5	4	1	3	**36**	14.4	36	0
Voeltzkowia rubrocaudata	3	3	1	5	**36**	36	0	10.3
** Zonosaurus quadrilineatus*	5	4	1	3	**36**	36	32	8
Ithycyphus oursi	3	3	1	5	**36**	0	36	0
** Liophidium chabaudi*	5	4	1	3	**36**	36	28.8	21.6
Madascincus igneocaudatus	3	2	1	5	**30**	12	30	0
Madagascarophis ocellatus	4	3	1	3	**28**	28	0	0
Blaesodactylus sakalava	3	1	1	5	**24**	24	16	0
Zonosaurus karsteni	3	3	1	3	**24**	24	24	0
Madagascarophis meridionalis	3	3	1	3	**24**	0	24	0
Trachylepis aureopunctata	3	2	1	3	**20**	6.7	20	3.3
Heteroliodon occipitalis	3	2	1	3	**20**	10	20	0
Leioheterodon geayi	3	2	1	3	**20**	20	0	0
Typhlops arenarius	3	2	1	3	**20**	0	6.2	20
Typhlops decorsei	3	2	1	3	**20**	0	20	0
Lygodactylus verticillatus	4	4	1	1	**16**	16	4	0
Phelsuma mutabilis	3	1	3	1	**16**	16	10.3	2.3
Amphiglossus ornaticeps	2	2	1	3	**16**	9.6	16	0
Oplurus cyclurus	2	2	1	3	**16**	16	6.5	0.73
Lygodactylus tuberosus	4	3	1	1	**14**	0	0	14
Paroedura picta	3	2	1	1	**10**	3.8	1.9	10
Furcifer verrucosus	3	2	1	1	**10**	10	2.9	0
Chalarodon madagascariensis	2	2	1	1	**8**	8	4	3.0
Trachylepis elegans	2	1	1	1	**6**	4.9	6	2.9
Dromicodryas bernieri	2	1	1	1	**6**	6	6	6
Mimophis mahfalensis	2	1	1	1	**6**	4.5	6	5.3
Hemidactylus mercatorius	1	1	1	1	**4**	4	3.4	2.9
Total conservation value of treatment						**514.7**	**542.8**	**112.7**

Table 5 Observed and estimated species richness and Conservation Value Index (CVI) score for birds and reptiles at three sites across a gradient of disturbance at Ranobe, southwest Madagascar.

	Low disturbance	**Moderate disturbance**	**High disturbance**
Observed bird richness	36	43	37
Estimated bird richness	42.0	46.8	39.7
Bird CVI	**856.4**	**825.7**	**478.6**
Observed reptile richness	27	27	15
Estimated reptile richness	30.5	34.2	19.1
Reptile CVI	**514.7**	**542.8**	**112.7**